Investigating behavior and ecology of Aphaenogaster swammerdami (Formicidae) in selectively logged forest: 20 years later – a happy ant?

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Investigating behavior and ecology of *Aphaenogaster swammerdami* (Formicidae) in selectively logged forest: 20 years later – a happy ant?

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Abstract

The impacts of logging have been widely studied at the community level, describing changes in species composition and richness, whereas the small-scale effects on behavior and ecology of single species have received less attention. We investigated whether the Malagasy wood ant *Aphaenogaster swammerdami* exhibits differences in colony density, colony size, and feeding ecology between three different sites within the Kirindy Forest (CNFEREF), a dry deciduous forest in central western Madagascar. Specifically, we compared undisturbed primary forest, a selectively logged area, and one site exposed to natural disturbance caused by an adjacent river. Transect surveys were used to record colony density as well as diameter of the mound as a predictor of colony size. Focal colonies were selected at all three sites to assess other aspects of colony size, i.e. the number and size of workers and the home range area. The feeding ecology of ants from all three sites was compared by using observational records on food quality and quantity, as well as stable isotope analyses of ant workers. We found that in selectively logged forest, colony density was lower and colony size larger than at the two other sites. Feeding behavior differed slightly, as colonies from selectively logged forest had a higher intake of animal food sources. Thus, we tentatively conclude that *A. swammerdami*, despite its opportunistic lifestyle, still exhibits responses to selective logging, which took place 20 years ago. Replicating these findings on a larger scale and determining the specific mechanisms leading to changes in lifestyle along disturbance gradients should be the focus of future studies.

Key words: anthropogenic disturbance, *Aphaenogaster*, Madagascar, Kirindy Forest, selective logging, stable isotope analysis

Résumé détaillé

Les impacts de l'exploitation agro-forestière sur des communautés d'espèces ont été étudiés en détail, et on a trouvé que l'exploitation sylvicole peut causer des changements dans la composition ou la richesse en espèces. Cependant, les changements à un niveau plus précis comme l'écologie ou le comportement d'espèces précises ont reçu peu d'attention. En conséquence, nous avons étudié l'impact de l'exploitation sylvicole semi-mécanisée sur la fourmi malgache, *Aphaenogaster swammerdami*. Pour cela, nous avons choisi trois sites dans la forêt sèche de l'Ouest de Madagascar à Kirindy (CNFEREF) : un site qui était exploité sélectivement il y a 20 ans, un site exposé aux perturbations d'une rivière adjacente et un autre site dans la forêt primaire. Un échantillonnage par transect a été utilisé pour déterminer la densité des colonies d'*A. swammerdami*. En même temps, le diamètre de chaque termitière a été mesuré pour estimer le nombre d'ouvrières de chaque colonie. Pour les investigations plus approfondies, six colonies focales sont choisis dans chaque localité. Pour ces colonies focales, nous avons mesuré le nombre d'ouvrières par la méthode de capture-marquage-recapture, la taille des ouvrières, et la taille de l'aire de nourrissage. Le régime alimentaire a été déterminé par des observations et par des analyses d'isotopes stables d'azote et de carbone des ouvrières de chaque colonie. Les résultats ont montré que la densité des colonies est plus faible dans la forêt exploitée que dans les autres sites. Pourtant, les termitières dans la forêt exploitée ont des diamètres plus grands et hébergent plus d'ouvrières. Le régime alimentaire est légèrement différent entre les sites : la proportion de nourriture d'origine animale est plus importante pour les colonies de la forêt exploitée. Ces résultats sont

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supportés par les dates d'analyses d'isotopes stables (le ratio de ^{15}N est plus grand dans les colonies dans la forêt exploitée). Nous n'avons pas trouvé des différences dans la surface de l'aire d'alimentation et la quantité de nourriture entre les sites. Mais, des différences entre les colonies occupant les trois sites ont été constatées. Bien que cette étude manque de réplicas, nous concluons provisoirement que *A. swammerdami* montre des réponses à l'exploitation semi-mécanisée de la forêt 20 ans après. Cependant, des études futures devront être menées pour vérifier la généralité de ces résultats en examinant plus de sites exposés à différent degré de perturbation et d'autres espèces de fourmis à Kirindy.

Mots clés : perturbation anthropogénique, *Aphaenogaster*, Madagascar, Forêt de Kirindy, exploitation sélective, analyse des isotopes stables

Introduction

From an evolutionary perspective, environmental disturbances are a two-edged sword because they not only lead to local ecological instability but also to new adaptations that ultimately contribute to the maintenance of biotic diversity (Darwin, 1859; Connell, 1978). However, in contrast to natural disturbances, anthropogenic interferences increased recently with the expansion of human populations into nearly every natural habitat on our planet. One example of anthropogenic disturbance that is assumed to have relatively low impact on the ecosystem is selective logging. It is considered as a sustainable alternative to clear-cutting as it allows the forest to recover and provides a long-term wood source of timber and fire wood from regrowth. Nonetheless, selective logging does have effects on species composition of animal communities (Magnusson *et al*., 1999; Sekercioglu, 2002; Peters *et al*., 2006; Edwards *et al*., 2011), forest structure (Uhl, 1989; Hall *et al*., 2003; Okuda *et al*., 2003), genetic diversity (Jennings *et al*., 2001) or nutrient cycling (Herbohn & Congdon, 1993). Although several studies have focused on the impact of selective logging on the behavioral ecology of mammals (Ganzhorn, 1995; Laurance & Laurance, 1996; Arnhem *et al*., 2008) and birds (Lambert, 1992; Chouteau, 2004), ecologically important groups of invertebrates remain poorly studied in this context. The present study contributes insight into the small-scale impacts of disturbances on colony density, size, and feeding behavior of a Malagasy ant.

Together with termites, ants are estimated to make up one third of the global animal biomass (Hölldobler & Wilson, 2009) and they influence their ecosystems in a variety of ways. Ants occupy different trophic levels as their feeding types range from herbivory to specialized predation (Tillberg *et al*., 2006). They can serve as pollinators (Beattie, 1985; Hölldobler & Wilson, 1990), seed dispersers (Böhning-Gaese *et al*., 1996) or as food source for other species (McNab, 1984). Ground-dwelling ants play a role in soil turnover and structure (Humphreys, 1981; Lobry de Bruyn & Conacher, 1994) as well as nutrient cycling (Levieux, 1983). Additionally, ants are often considered as bio-indicators (Andersen, 1997; Majer, 1983). Several studies indicated that selective logging does not have an impact on ant species richness (Olson & Andriamiadana, 1996; Vasconcelos *et al*., 2000) but there is some evidence that it alters species composition (Punttila *et al*., 1991; Kalif *et al*., 2001; Dunn, 2004; Widodo *et al*., 2004).

Species composition and richness of a given habitat depend on the ecological flexibility of single species making up the community. Species-specific responses of ants to selective logging can help us understand how species recover from or adapt to particular disturbances, which can be considered agents of natural selection (Sousa, 1984). As mentioned above, although the responses of ant communities to logging have been studied, little is known about how morphological, behavioral, and life history traits of single species are affected by this anthropogenic disturbance.

On a species level, logging appears to have a negative impact on population densities in some species (Olson & Andriamiadana, 1996; Vasconcelos *et al*., 2000; Sorvari & Hakkarainen, 2007), whereas it enhances population growth in others (Walsh *et al*., 2004). For example, mounds of *Formica rufa* were found to be smaller after logging (Domisch *et al*., 2005), and Sorvari & Hakkarainen (2009) found individual ants to be smaller in logged forest, probably due to nutritional deprivation. There has been some discussion about how ants should adapt to disturbances. Kaspari & O'Donnell (2003) suggest that severe disturbances would select for smaller colonies, which could also result in shorter generation times (Linksvayer & Janssen, 2009). In addition to this 'r-strategy', small colonies favor low queen-worker dimorphism, which could result in polygyny instead of investing in a single egg-laying queen that could be killed during frequent disturbances (Linksvayer & Janssen, 2009). In contrast, some species invest in colony growth rather than reproduction to cope with disturbances (i.e. competitors or predators)

(Linksvayer & Janssen, 2009). However, a small number of unspecialized workers seem to be more advantageous to deal with disturbances than a large number of specialized workers albeit even these can exhibit task redundancy (Wilson, 1984). Obviously, different species vary in their response to disturbances. For example, it was shown that anthropogenic disturbances, such as fire, facilitate the colonization by a dominant species to some degree (Gibb & Hochuli, 2003), indicating that disturbances can indeed be advantageous for opportunistic species that are able to adapt to the altered environments.

Madagascar, being one of the global hotspots of biodiversity, shelters vast numbers of endemic species (Myers *et al*., 2000). About 96% of the 1000 described Malagasy ant species are endemic, but probably only about one fourth of the island's species have been named (Fisher, 2003). The dry forests of western Madagascar with their 86 known ant species are species-rich compared to other localities (Olson & Ward, 1996). Our study took place in Kirindy Forest (CNFEREF), where selective logging (for *Commiphora* spp.) started in 1987 (Ganzhorn, 1995). Studying the impact of tree extraction on ants 5 - 10 years after selective logging, Burkhardt *et al*. (1996) detected a slightly higher number of overall ant species in the selectively logged area, whereas the number of ground-dwelling species, in particular, was lower.

One of these ground-dwelling species is *Aphaenogaster swammerdami* (Forel 1886) of the Family Formicidae, for which colonies were significantly less abundant in the selectively logged forest (Burkhardt *et al*., 1996). This abundant species lives in large underground nests that have one large entrance hole and conspicuous mounds (Böhning-Gaese *et al*., 1999). Outside Madagascar, the genus *Aphaenogaster* is found on all continents and it has been studied in the Mediterranean (Cerdà *et al*., 2009; Galarza *et al*., 2009), North America (Hölldobler *et al*., 1978; Sanders & Gordon, 2002; Tschinkel, 2011), Central America (McGlynn *et al*., 2003, 2004), and Australia (Shattuck, 2008). As its congeners, *A. swammerdami* seems to be omnivorous. In Madagascar, this species plays an important role in the secondary dispersal of seeds of the Malagasy tree *Commiphora guillaumini* (Böhning-Gaese *et al*., 1996). However, little is known about the lifestyle of *A. swammerdami*.

The aim of this study was to determine differences in the ecology and behavior of *A. swammerdami* between logged forest and two control sites consisting of undisturbed primary forest and another unlogged site exposed to natural disturbance by an adjacent river. Specifically, we asked: (1) Do colony density and size parameters (worker number, worker size, mound diameter, and home range) differ between the three sites? (2) Does the feeding behavior of colonies differ between habitat types with respect to dietary composition and quantity?

Materials and methods

Study site and forest characteristics

Data were collected from March to May 2011 in the Kirindy Forest, a dry deciduous forest in western Madagascar, approximately 60 km northeast of Morondava (44°39'E, 20°03'S, 30 - 60 m asl). The study site is located within a 12,500 ha forest concession of the Centre National de Formation, d'Etude et de Recherche en Environnement et Foresterie (CNFEREF) de Morondava. Kirindy Forest is characterized by a dry season of 6 - 9 months and a rainy season between December and February (Sorg & Rohner, 1996). Between 1987 and 1990, selective logging of large trees of *Commiphora guillaumini* (Burseraceae; local Malagasy name *arofy*) occurred in selected parts of the forest (Sorg *et al*., 2003). We collected data at three different sites: (1) partly selectively logged around 1987 (SL) as well as (2) an immediately adjacent unlogged site (adjNL) and (3) another unlogged site about 2 km away adjacent to the Kirindy River (rivNL) (Figure 1). The latter site was chosen as an additional control site for natural disturbances due to the river as *A. swammerdami* seems to be sensitive to variation in soil humidity (Burkhardt *et al*., 1996).

Unpublished data (F. Koch, C. Großheim) of forest density and composition were used to assess forest characteristics of the study sites. This analysis revealed that the number of trees per hectare did not differ among the three study sites (ANOVA, n = 60 randomly chosen squares of 400 m², F (2, 57) = 1.88, P = 0.162). Selective logging reduced the number of *Commiphora* trees per plot in NL as compared to the two unlogged sites (*post-hoc* tests: SL – adjNL: U = 10539, P < 0.001; SL – rivNL: U = 36498, P < 0.001; rivNL – adjNL: U = 46223, P = 0.122). The number of *Commiphora* in SL was reduced by 75 - 87% in comparison to the two unlogged sites.

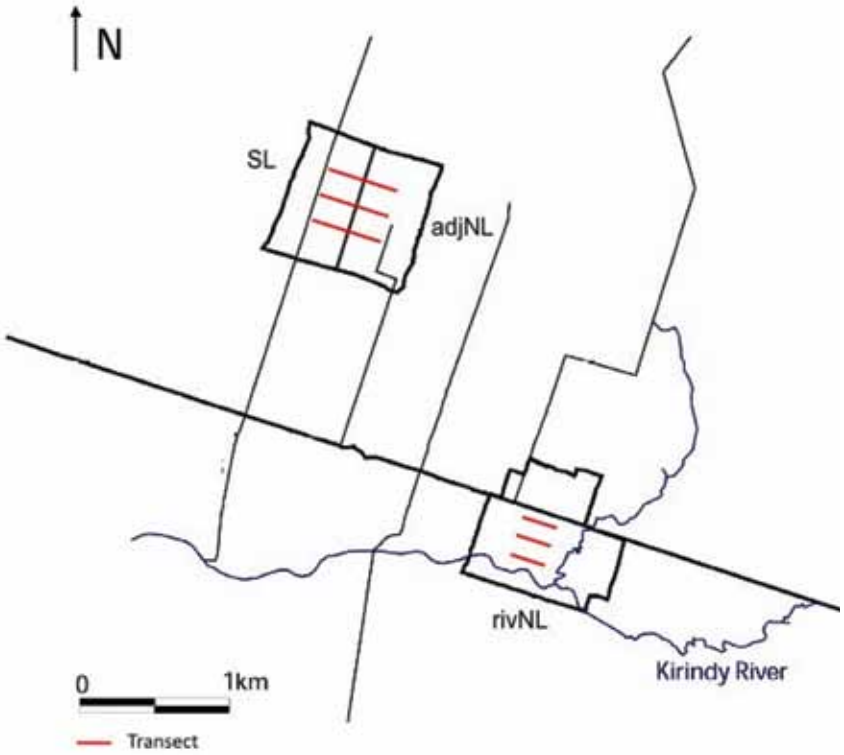

Figure 1. Overview over the study area in the Kirindy Forest (CNFEREF) and transects at each of the three sites: selectively logged (SL) and unlogged (adjNL) areas in the north and unlogged rivNL close to Kirindy River.

Transect surveys

In each area, three transects were conducted on small trails, intersecting both selectively logged and unlogged forest in SL and adjNL (Figure 1). The minimal distance between transects was 120 m in rivNL and 180 m in SL and adjNL. During surveys, colonies within a distance of 15 m on each side of the transect were counted and their perpendicular distance to the transect line was measured. Transects covered a total length of 726 - 836 m. To determine the colony density of *A. swammerdami* the following formula was used:

$$D = N \sqrt{(2N / \pi \sum_i (d_i^2))} / (2L)$$

(D = density, n = total number of colonies detected, d_i = perpendicular distance of colony to transect line, L = transect length (Sutherland, 2006, pp. 147))

The mound diameter of each detected colony was measured as mound size is assumed to be a reliable predictor of colony size (Tschinkel *et al*., 1995).

Further, for each of the three plots, six focal colonies were chosen randomly by selecting two colonies from each of the three transects. As a small-scale measurement of colony density, the distance of neighboring *A. swammerdami* colonies within a radius of 20 m were determined for each focal colony.

Estimation of worker numbers

The Jolly-Seber capture-mark-recapture method (Krebs, 1999) was applied for all 18 focal colonies to determine the number of foragers. To capture the ants a wooden stick of approximately 30 cm length with a diameter of 5 mm was held into the entrance hole of a colony for 10 sec after which the individuals climbing up the stick were transferred into a jar. For each capture session, this procedure was repeated 20 times within 5 min. All caught ants were marked with waterproof color on the thorax (Edding 751 Paint Marker, Edding International GmbH, Ahrensburg, Germany). In total, 61 - 151 individuals were marked per colony. Marked individuals were released three hours after the capture at the nest entrance. The recapture procedure was the same as the capture procedure explained above. The entire capture procedure for one colony occurred at the same hour during three consecutive days (three capture sessions) and was carried out on different days than the determination of home ranges and observations.

Home ranges

The home range of each focal colony was determined by assessing locations of single individuals foraging in the immediate surroundings of the nest. Each randomly encountered individual was presented a

piece of rice to observe the homing of the animal. As the maximum seed dispersal distance has been recorded to be 10.4 m (Böhning-Gaese *et al*., 1999), we presented rice within a radius of 15 m from the nest entrance. In total, we collected 27 to 32 locations for each colony within one or two consecutive days of similar weather conditions (e.g. not during or after strong rain), and evenly split between morning and afternoon. Home range size was determined by calculating the area of the minimum convex polygon of all assessed data points, using the ArcView 3.1 GIS software (ESRI, Redlands, CA, USA).

Worker size and weight

To estimate body size 40 - 47 workers were collected from each focal colony by the same method used for the capture-mark-recapture procedure. The body length of each individual was measured from the tip of the mandibles to the most posterior point of the abdomen (precision 0.5 mm). To estimate worker weight and thereby biomass, six individuals of each colony were oven-dried and weighed to the nearest µg with an analytical balance. Biomass was approximated by multiplying the site-specific estimated number of workers by the site-specific mean weight of the workers by the colony density for each of the three sites.

Observations on feeding ecology

Each colony was observed on four different days, each observation period being one hour, and at four different times of the day (07h 30 - 10h, 10h - 12h 30, 12h 30 - 15h, 15h -17h 30) in a randomized order. During observations, category and size of each food item transported into the nest entrance was noted (categories: insect, other invertebrate, vertebrate, fungus, plant, miscellaneous).

Stable isotope analysis

The ratios of stable isotopes of chemical elements can be used to investigate ecological relationships among organisms such as food webs. Stable nitrogen (^{15}N) can serve as a tracer to estimate the trophic position of organisms because it is enriched by ca. 3‰ in consumers relative to their diet (Post, 2002). Enrichment in stable carbon (^{13}C) is smaller, ca. 1‰, and this isotope provides information on the number of basal resources entering a food web (Post, 2002). We applied stable isotope analysis to investigate two aspects of the feeing behavior of *A. swammerdami*: (1) We aimed at determining the trophic level of this species, i.e. its position in the food web via stable nitrogen and (2) we tested for differences in isotope ratios between sites to investigate whether the diets of the focal colonies differ in composition between sites.

For the stable isotope analysis on average 8 (range 1 - 12) ants were collected from each focal colony, stored in 100% ethanol for four weeks and oven-dried at 60°C for three days prior to stable isotope analysis. Legs and thorax were used for the analysis to avoid artifacts associated with ingested food in the abdomen and head. Further, we determined the habitat baseline of the sampled ants using two common tree species (*Diospyros tropophylla*, Ebenaceae: $n_{rivNL} = 20$, $n_{adjNL\ \&\ SL} = 15$ and *Securinega seyrigii*, Euphorbiceae: $n_{rivNL} = 19$, $n_{adjNL\ \&\ SL} = 20$). Leaves were collected, immediately dried in the sun, and stored without any preservative. Leave samples were ground and homogenized with a ball mill before stable isotope analyses. Analyses were carried out by the Center for Stable Isotope Research & Analysis (KOSI), Göttingen, using an isotope ratio mass spectrometer (Delta Plus, Finnigan MAT, Bremen, Germany) in an online-system after passage through an element analyzer (NA 1110, Carlo Erba, Milan, Italy).

Data analysis: Observational data

All measured variables were tested for normal distribution by performing Shapiro-Wilk tests. To compare mound sizes of colonies among sites we used an ANOVA and *post-hoc* pair-wise comparisons via Tukey's-HSD tests. Parameter recorded for the 18 focal colonies (number of workers, number of food items brought into the nest, home range area, worker size) were compared among the three sites using Kruskal-Wallis tests, followed by Mann-Whitney-U tests for pair-wise comparisons. We used Spearman correlations to determine relationships between single variables using data from the 18 focal colonies. Significance levels of non-parametric post-hoc tests were adjusted according to the Holm-Bonferroni correction (Holm, 1979). All other significance levels were set at $P \leq 0.05$. All statistical analyses were carried out in R 2.15.0.

Data analyses: Stable isotope analysis

We compared stable nitrogen and stable carbon signatures of individuals among sites using ANOVA / Kruskal-Wallis test with corresponding *post-hoc* tests. Analyses were carried out for both absolute values

and relative values corrected for the habitat specific baseline of both tree species.

Results

Transect surveys and colony density

Mound diameter of all colonies detected during the transect surveys differed between the three sites and were largest in logged forest (F = 75.72, $P < 0.001$; *post-hoc tests*: all $P < 0.001$) (Figure 2A). Mean colony density in NL was lowest with 0.028 colonies per meter transect, in contrast to almost ten fold higher densities of 0.201 in adjNL and 0.205 in rivNL (Figure 2A). The distance of the nearest neighbor colony did not differ among sites ($\chi^2_{2df} = 2.15$, $P = 0.34$), though the median distance was highest in SL and significantly higher than in rivNL (*post-hoc* test: U = 36, $P = 0.005$), supporting the findings from the transect surveys, which indicate that SL had the lowest colony density.

Comparison among study sites

Overall, the estimated number of workers per colony differed among the three sites ($\chi^2_{2df} = 8.51$, $P = 0.014$). Colonies in SL contained more workers compared to adjNL (*post-hoc* test: U = 34, $P = 0.013$) and rivNL (U = 33, $P = 0.020$) (Figure 2B). Home ranges, which were roughly circular around the nest entrance, showed a difference in area close to significance between the three sites ($\chi^2_{2df} = 5.49$, $P = 0.064$). Home ranges were significantly smaller in rivNL than in SL (*post-hoc* test: U = 0, $P = 0.002$) (Figure 2C). Mean worker size was highest in SL

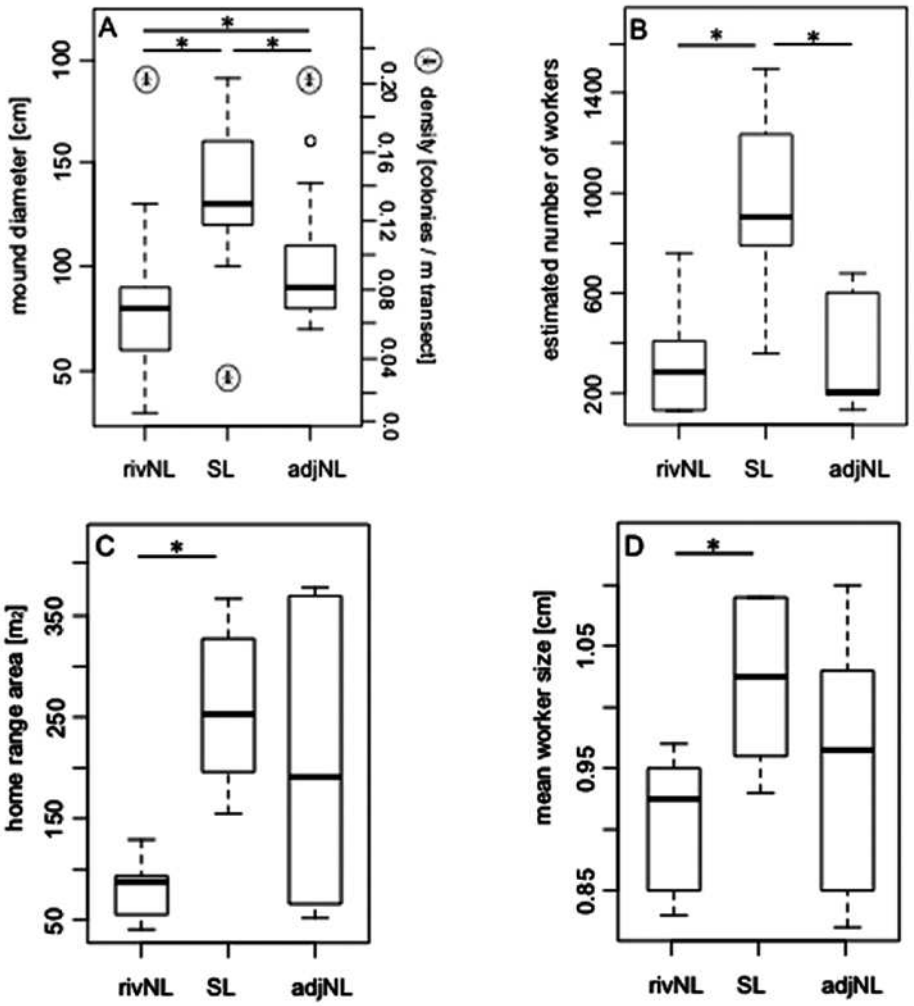

Figure 2. A) On the left axis: mound diameters of colonies detected on three ca. 250-m transects per site (rivNL: 96 colonies, SL: 22 colonies, adjNL: 68 colonies). Box plots indicate median, upper and lower quartiles, as well as minimum and maximum values, circles indicate outliers. On the right axis: mean site-specific colony density (in colonies per meter transect) of each three transects per site. B) Estimated number of workers per colony of the focal colonies plotted by site (n = 6 colonies per site). C) The home range area of the focal colonies plotted by site (n = 6 colonies per site). D) Mean size of the workers for all three sites (n = 6 colonies per site). Significant differences ($P < 0.05$) are indicated by asterisks.

and differed significantly from rivNL (*post-hoc* test: U = 32, P = 0.030) (Figure 2D). Food intake and the distance of the nearest neighbor did not differ among sites (P > 0.1).

As some variables of the 18 focal colonies were correlated with the estimated number of workers, comparisons between sites were also performed with residuals from these correlations to control for colony size. Residuals of the correlations with the estimated number of workers did not differ among sites for home range area (χ^2_{2df} = 4.43, P = 0.11), worker size (χ^2_{2df} = 1.82, P = 0.53) and number of food items brought into the nest per hour (food intake) (χ^2_{2df} = 1.82, P = 0.40).

Correlations between characteristics of focal colonies

The estimated number of workers correlated positively with mound size (n = 18, R_s = 0.68, P = 0.002). Additionally, mound size correlated positively with home range area, food intake, worker size, and worker weight (R_s > 0.63, P < 0.01). By multiplying colony density by the site-specific average number of workers per colony and the average dry weight of the workers, we assessed ant biomass. As the minimal recorded number of workers within a colony was around 200 individuals, this value was used as a proxy for colonies in rivNL as the calculation using their mean mound diameter resulted in negative values. The calculations revealed a biomass of 0.06 g/m transect in rivNL, 0.22 g/m in adjNL, and 0.22 g/m in SL.

Feeding ecology: Observational data

Colonies in rivNL had a lower intake of insects (χ^2_{2df} = 49.2 P < 0.001) and a higher intake of fungi (χ^2_{2df} = 7.8, P = 0.02) compared to adjNL and SL (Figures 3 & 4). There were no differences among colonies for

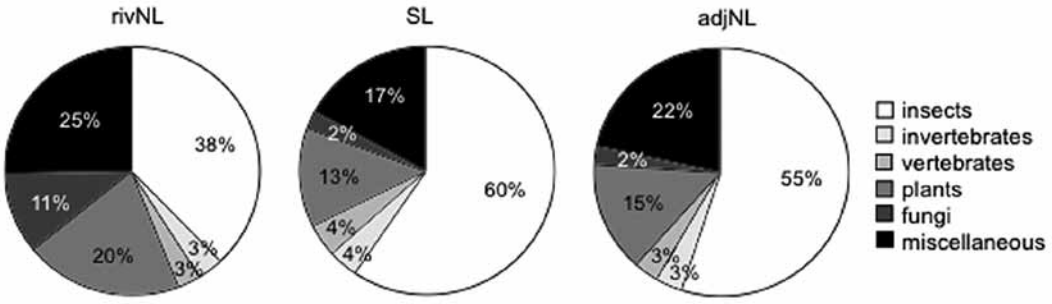

Figure 3. Mean proportions of the food categories of items brought into the nest during 4 hours of observation per colony (n = 6 colonies for each site).

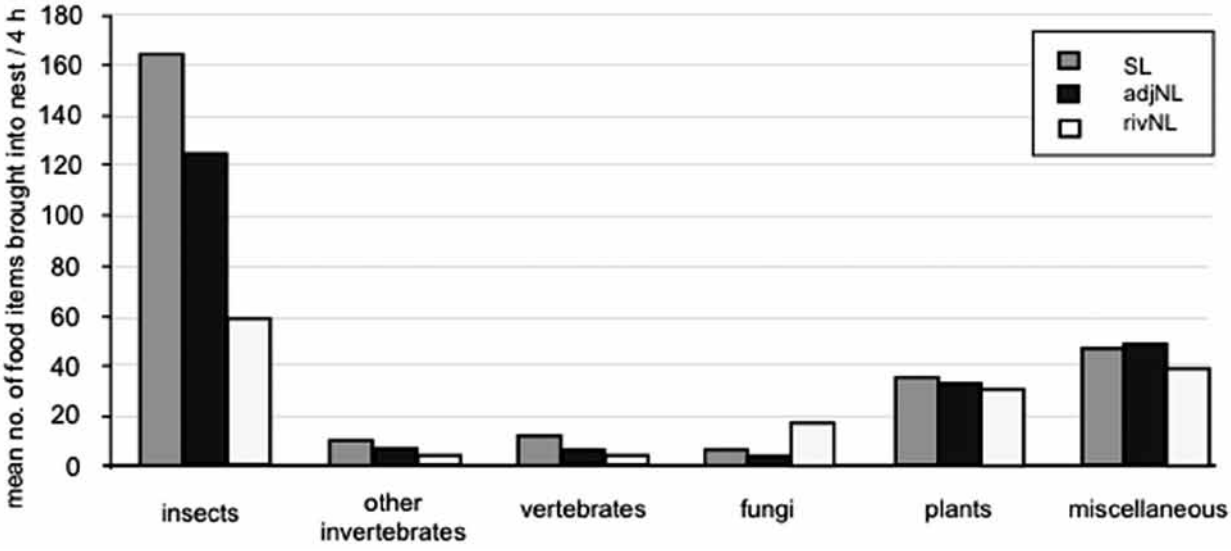

Figure 4. Mean food intake for all 18 focal colonies. The Y-axis corresponds to the number of items brought into the nest entrance during the entire 4 hours of observation per colony, the X-axis corresponds to the recorded food categories.

all other food categories (all $P > 0.1$). During 72 hours of observation, only one dispersal of a *Commiphora guillaumini* seed was observed.

Feeding ecology: Stable isotope analysis

The stable isotope habitat baseline differed between rivNL and SL and adjNL in $\delta^{15}N$ but not in $\delta^{13}C$ for both tree species (*Securinega seyrigii*: rivNL: $\delta^{15}N = 6.18 \pm 0.85$, $\delta^{13}C = -28.7 \pm 0.70$; SL and adjNL: $\delta^{15}N = 11.5 \pm 0.97$, $\delta^{13}C = -28.5 \pm 0.70$; *Diospyros tropophylla*: rivNL: $\delta^{15}N = 7.2 \pm 0.71$, $\delta^{13}C = -30.1 \pm 0.61$; SL and adjNL: $\delta^{15}N = 11.7 \pm 1.51$, $\delta^{13}C = -30.0 \pm 0.62$). For *A. swammerdami*, comparison of absolute $\delta^{13}C$ values between sites revealed lower values in rivNL compared to SL and adjNL, but no difference within SL and adjNL ($F = 14.9$, $P < 0.001$; *post-hoc* tests: rivNL – adjNL and rivNL – SL: $P < 0.001$; SL – adjNL: $P = 0.84$) (Figure 5A). $\delta^{15}N$ values differed between all sites ($\chi^2 = 121.5$, $P < 0.001$; *post-hoc* tests: all $P < 0.001$) (Figure 5B). When stable carbon values were corrected for the habitat specific baseline of *Diospyros tropophylla*, difference between rivNL and SL and adjNL remained ($F = 5.44$, $P = 0.005$; *post-hoc* tests: rivNL – adjNL: $P = 0.007$; rivNL – SL: $P = 0.050$; SL – adjNL: $P = 0.84$), however, when corrected for the baseline of *S. seyrigii* no difference could be found between sites ($F = 0.73$, $P = 0.49$). Baseline correction of stable nitrogen data for both tree species revealed significantly higher $\delta^{15}N$ values in rivNL and SL compared to adjNL (*S. seyrigii*: $F = 57.1$, $P < 0.001$; *post-hoc* tests: rivNL – adjNL and adjNL – SL: $P < 0.001$; SL – rivNL: $P = 0.22$; *D. tropophylla:* $F = 41.9$, $P < 0.001$; *post-hoc* tests: rivNL – adjNL and adjNL – SL: $P < 0.001$; SL – rivNL: $P = 0.06$) (Figure 6)

Discussion

The aim of this study was to explore and quantify variation in behavior and ecology of the Malagasy wood ant *Aphaenogaster swammerdami* among field sites with different sylvicultural histories: one site was selectively logged 20 years earlier (SL), one site consisted of unlogged relatively intact forest (adjNL), and a third site was unlogged but exposed to disturbances due to an adjacent river (rivNL). The two unlogged sites appeared rather similar to one another as compared to the logged site. We found that colonies in SL were larger but less abundant compared to the two unlogged sites (adjNL, rivNL). The estimated biomass in SL and adjNL were four times higher as compared to rivNL, but did not differ within the two sites. Food composition differed slightly between sites in terms of fungi and insects; this factor was additionally highlighted by stable isotope analysis.

Do colony density and size parameters differ among the three forest sites?

Colony densities in unlogged forest were ten times higher than in selectively logged forest. Though there was no difference in tree density, the logged area by

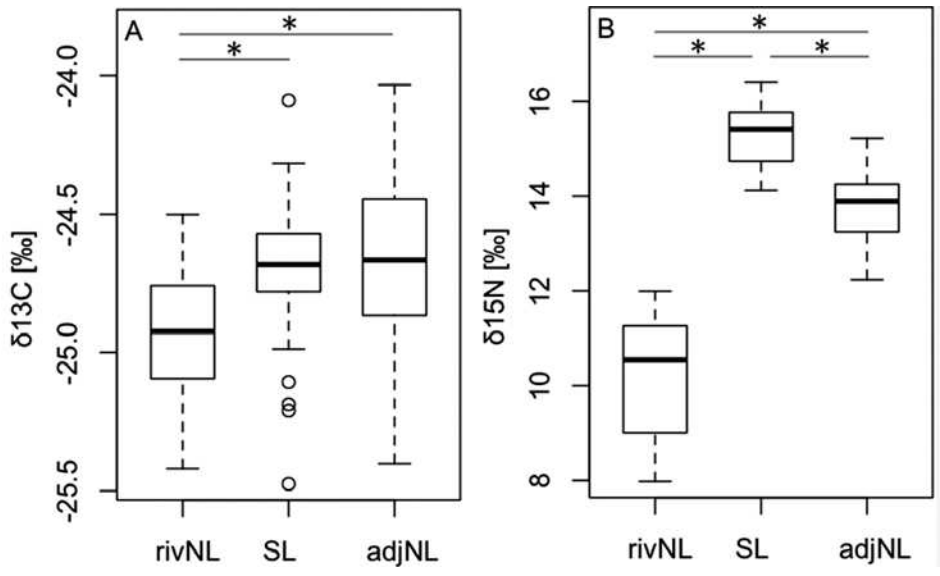

Figure 5. A) Stable carbon isotope values ($\delta^{13}C$) of ants of the three study sites (n = 210 individuals). Plotted are median, upper and lower quartiles as well as minimum and maximum values. B) Stable nitrogen values ($\delta^{15}N$) of ants of the three study sites (n = 145 individuals). Significant differences ($P < 0.05$) are indicated by asterisks.

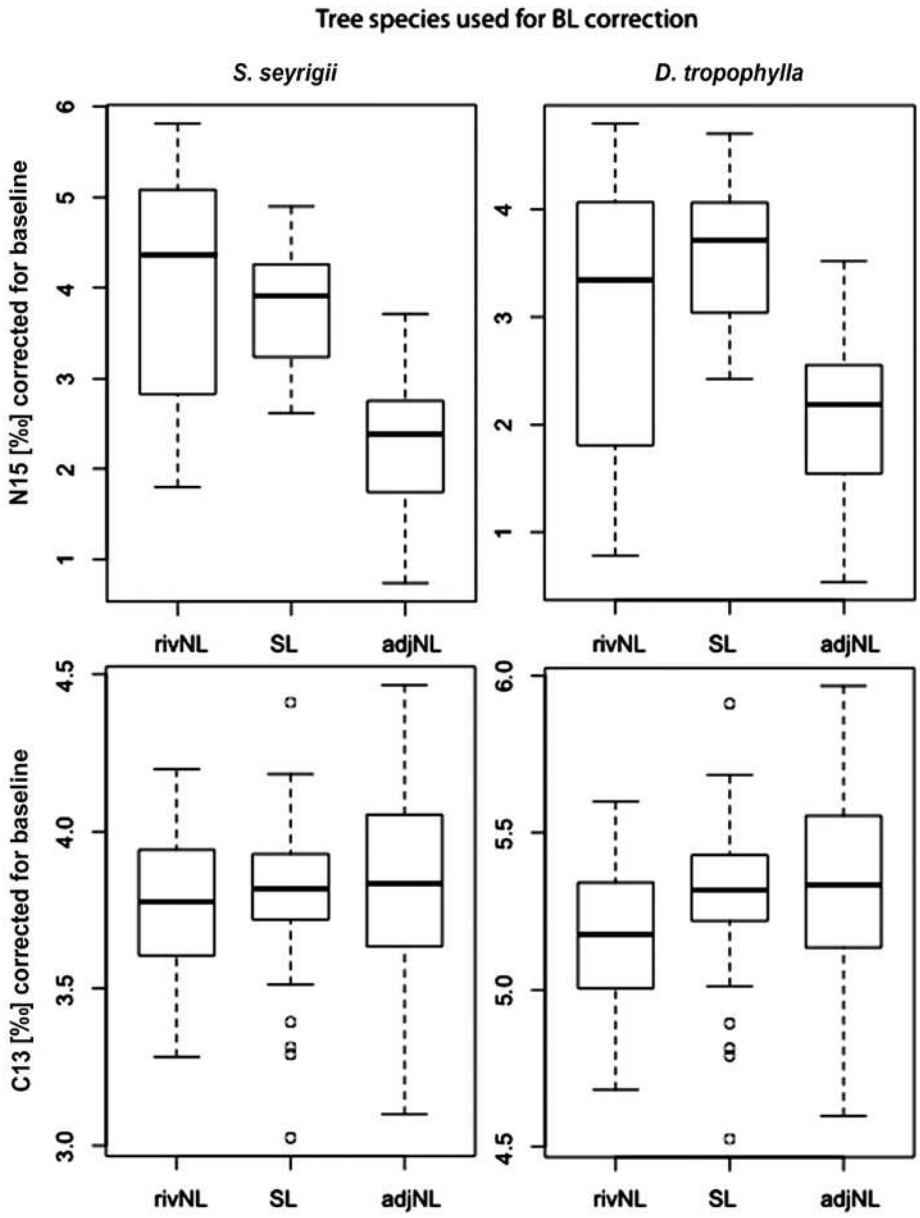

Figure 6. Values of stable nitrogen and carbon values of ants corrected for the site specific habitat baseline assessed from two tree species (*Securinega seyrigii* and *Diospyros tropophylla*).

definition lacks *Commiphora guillaumini* trees, which could explain the lower abundance of colonies at the SL site. *Aphaenogaster swammerdami* acts as a seed disperser for *C. guillaumini* and feeds on the arils of the seeds (Voigt *et al.*, 2002). Surprisingly, the dispersal of seeds of *C. guillaumini* was observed only once even though this study was carried out during the fruiting season of this tree. Thus, *A. swammerdami* does not seem to depend on *C. guillaumini* seeds as a major food source and the low colony density might be due to other factors. One possible explanation for the differences in density could be increased pressure due to competition with *Pheidole* spp., which has been found to influence negatively *A. swammerdami* (Burkhardt *et al.*, 1996). However, this explanation remains speculative, as we did not assess the abundance of *Pheidole* spp. Nonetheless, the finding of decreased ant population densities in selectively logged forest is in agreement with other studies (Olson & Andriamiadana, 1996; Vasconcelos *et al.*, 2000; Sorvari & Hakkarainen, 2007).

Colony size was largest in selectively logged forest, where density was lowest. In addition, colonies in the selectively logged forest had the largest home ranges and the highest food intake – two parameters highly dependent on colony size (Tschinkel *et al.*, 1995). These findings can be

explained by two factors: 1) competition between colonies might increase with colony density. *Aphaenogaster swammerdami* seems to maintain rather exclusive territories and home ranges do not appear to overlap (unpublished data). It is therefore likely that colony size is limited by neighboring nests, which would explain why colonies in SL could grow to a maximum size. This limitation might be due to an effect of saturation in the unlogged sites where the carrying capacity of *A. swammerdami* might be reached in contrast to the selectively logged area. 2) colony and worker size might depend on nutrient availability and quality. According to Kaspari (2005), positive correlations between food supply, as well as growth in worker body mass and number, have been found. However, increased growth due to a higher food supply at the logged site would be contradictory to the lower colony density as in that case one would expect an overall growth of the population, not only within colonies.

The estimated biomass of *A. swammerdami* did not differ between selectively logged and unlogged forest in SL and adjNL. Nevertheless, it was nearly four times lower in rivNL, which might be associated with a higher risk of flooding by the nearby river. Though one has to consider that the biomass of *A. swammerdami* was only roughly estimated, this finding suggests that the impact of the river as a natural source of disturbance (flooding, higher soil humidity) might actually be higher than the one of selective logging.

Another explanation for the lower biomass in rivNL could, again, be the constant competition with *Pheidole* spp., which were found to be more abundant in this area of the Kirindy Forest in 1995 (Burkhardt *et al*., 1996) and were observed to force *A. swammerdami* colonies to leave their nests (J. Burkhardt, unpublished data). This pressure due to inter-specific competition might result in a higher frequency of *A. sammerdami* colonies moving from one nest to another, perhaps resulting in smaller colonies and individuals, which would decrease their biomass.

Does the feeding behavior of colonies differ among sites with respect to composition and quantity?

The observational data revealed that all colonies exploit the same food categories. However, these categories were defined at broad taxonomic levels, such as Kingdoms or Phyla and it is possible that the diet between sites differed on a more precise taxonomic level. Only minor differences could be found in the quantitative composition of the diet. Colonies in the unlogged forest of rivNL fed on more fungi than in SL and adjNL. As rivNL is adjacent to the Kirindy River, this effect can possibly be explained by higher soil humidity and, hence, higher fungus growth.

The observational data also revealed that the diet of colonies in SL and adjNL included more insects, a finding supported by the stable isotope analysis (absolute $\delta^{15}N$ values were 4 – 5‰ higher in SL and adjNL). When corrected for the site specific habitat baseline, $\delta^{15}N$ is significantly lower in adjNL compared to SL and rivNL. This indicates that, within SL and adjNL, the diet of ants in logged forest was composed of more material from higher trophic levels, i.e. animal tissue.

This effect could have two possible explanations: (1) the availability of plant-derived food is lower in SL. With regard to selective logging, this would be true for *C. guillaumini* trees though this study could not find observational evidence for a high dependence of *A. swammerdami* on *C. guillaumini* seeds. Alternatively, it is possible that the availability of faunal food sources is higher in SL compared to adjNL, whereas the abundance of plant-derived food sources is equal. (2) It is possible that the deviation in $\delta^{15}N$ is due to a difference in foraging behavior and competitive ability. One could argue that the larger ants / colonies in SL are superior competitors. Nevertheless, the diet of all colonies was mainly composed of very small items below 1 cm, including insects such as termites, ants, and larvae, which would not be easier to subdue with increasing body or colony size.

The storage of specimens in ethanol can lead to shifts in ^{13}C values in stable isotope analysis (Tillberg *et al*., 2006). Hence, these results have to be interpreted cautiously. However, all specimens underwent the same storage conditions, which would lead to a similar bias in all samples without affecting the relative differences between them. As the main focus of the stable isotope analysis was to determine the trophic level based on ^{15}N values, which are not affected by storage in EtOH.

In addition to the results on the differences among forest sites, this study provided new insights into the lifestyle of *A. swammerdami*. The estimated colony sizes are in agreement with results obtained from other *Aphaenogaster* spp., whose average number of adult individuals per colony ranges between 100 and 700 (Hölldobler & Wilson, 1990; Tschinkel, 2011). In general, the ecology of *A. swammerdami* seems to

be comparable to it congeners, which live in colonies in the soil with a single large entrance hole, disperse seeds from different plants, and are omnivorous (Sanders & Gordon, 2002; McGlynn *et al*., 2003; Ness *et al*., 2009; Boulay *et al*., 2010). The stable isotope analysis revealed that this species covers approximately two trophic levels (^{15}N values lie 0.6 - 5.4‰ above the habitat baseline) and exhibits high individual differences in diet, which can be explained by an omnivore lifestyle – a finding supported by the observational data. As found in other ant species that feed on uniformly distributed and continuously renewing resources (Hölldobler & Wilson, 1990), the home ranges of *A. swammerdami* extended more or less circularly around the nest entrance and are established by solitary foragers.

Linksvayer & Janssen (2009) stated that species that have the least difficulties to cope with disturbances are mainly opportunists, which in ants are characterized by small colony size, unspecialized morphology and behavior, unspecialized diet, and nest sites, as well as polygyny and polydomy. *Aphaenogaster swammerdami* meets most of these expectations (except for polygyny and polydomy, as we have no information at this time on breeding systems) and, therefore, it is classified as an opportunistic species. Hence, it should be adapted to cope with disturbances. Our results revealed clear divergences among sites exposed to different levels of disturbances, but we cannot conclusively assign these differences to adaptations to selective logging or soil humidity. Without replication of these experiments at additional sites, the mechanisms leading to the differences described herein remain unknown. Differences between logged and unlogged forest should not be reduced to sylvicultural management, as they could simply mirror a geographic effect. Therefore, as our results are descriptive, future research should focus on extending this dataset by investigating other sites exposed to different kinds of disturbances to find a general pattern.

This study has provided interesting insights into the life history of *A. swammerdami*, although information about other ant species inhabiting the Kirindy Forest are lacking. Sensitive ant species that have a less opportunistic life style might show completely different or stronger responses to disturbance. This might in turn be advantageous for *A. swammerdami* as it could reduce competition from other ant species at disturbed sites. This in turn could explain why colonies in logged forest were larger compared to colonies in unlogged forest. Several studies show that disturbances can indeed favor (re-) colonization of ecologically dominant species that alter the composition of a community or even replace other, less adaptable species (Fox & Fox, 1982; Gibb & Hochuli, 2003).

Despite certain limitations, this study highlights that research on disturbance ecology should not only focus on effects at the community level but also on single species as changes in their lifestyles may impact the entire ecosystem and are the first signals to indicate alterations in species composition.

Conclusion

This study of the ecology and life history of *Aphaenogaster swammerdami* revealed significant differences between forest sites with different levels or histories of disturbance. In particular, colonies in parts of the forest that were selectively logged 20 years earlier were larger and fed on slightly more animal derived food, indicating that these ants respond to subtle variation in habitat quality. Our study also contributes new knowledge on the functional ecology of this ant species. Even though a lack of replication renders some conclusions preliminary, our study suggests that the effects of selective logging can be subtle and long lasting for particular species. This can be tested in future studies that examine single species across disturbance gradients, which would ultimately allow identifying the mechanisms leading to alterations in local species composition.

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